Predation on the Apple Snail, *Pomacea canaliculata* (Ampullariidae), by the Norway Rat, *Rattus norvegicus*, in the Field

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Abstract. Aspects of predation on the apple snail, *Pomacea canaliculata*, an important pest of rice, by the Norway rat, *Rattus norvegicus*, were studied near a drainage canal in southern Japan. Most of the shells attacked by the rats were broken in a characteristic way, from the outer edge of the last whorl up to the attachment site of the columellar muscle. The rats ate all the flesh of the snails except for the albumen gland of the female. They preferred *Pomacea canaliculata* to another freshwater snail *Semisulcospira libertina*. They preferred large *Pomacea* snails to small ones but showed no preference between the sexes of the snails. The numbers of snails attacked within 12 hours varied from 0–12 per rat hole, and predation was almost always nocturnal.

INTRODUCTION

The apple snail, *Pomacea canaliculata* (Lamarck, 1804), was introduced into Asia from South America mainly in the 1980's as food for humans (Halwart, 1994a, b; Wada, 1997). However, its commercial value was soon lost, and abandoned snails became wild in many Asian countries including Cambodia, China, Indonesia, Korea, Japan, Laos, Malaysia, Taiwan, Thailand, Papua New Guinea, the Philippines, and Vietnam (Halwart, 1994a, b; Somony, 1998). Areas infested by this snail in these countries are still expanding (Wada, 1997), and other neighboring countries (e.g., India and Australia) are threatened with invasion (Baker, 1998). *P. canaliculata* feeds voraciously on rice seedlings and has now become one of the most important pests of rice in Asia.

Due to difficulties in applying chemical and cultural techniques to control this snail, natural enemies have been suggested as biological control agents (Kondo & Tanaka, 1989; Halwart, 1994a, b; Wada, 1997). In addition, proper understanding of the population dynamics of the snail in the field depends in part on identifying the influence of predation on snail numbers. Until now, several wild animals have been observed to feed on *Pomacea canaliculata* (Hamada & Matsumoto, 1985; Kondo & Tanaka, 1989; Ozawa et al., 1989; Halwart, 1994a, b; Chanyapate, 1997; Suzuki et al., 1999), but few of these predators attack adult snails (but see Ozawa et al., 1989). No attempts have been made to quantify predation on this snail by wild animals in natural habitats.

Rodents have been observed feeding on *P. canaliculata* in Thailand (Chanyapate, 1997) and the Philippines (Almazan et al., unpublished data). In March 1998, piles of broken shells of this snail, apparently attacked by a species of rodent, were found near a drainage canal in

southern Japan. Using video recordings, we identified the rodent to be the Norway rat, *Rattus norvegicus* (Berkenhout, 1769). In this paper, we report aspects of this rat's predatory behavior and discuss the influence of its predation on snail numbers.

MATERIALS AND METHODS

Study Area

The canal along which we found many broken shells of *P. canaliculata* was in Shichijo, Kumamoto Prefecture, Kyushu Island, southern Japan (130°50′E, 33°10′N). The water in the canal was 1.5 m wide and approx. 0.3 m deep. Both sides of the canal were lined with concrete walls (0.5 m high), above which soil banks extended 2 m farther. The bottom of the canal was also lined with concrete, but sand and pebbles completely covered this.

Four rat holes, two on each side of the canal, were dug into the soil banks just above the concrete walls of the canal. The two holes on each side were approx. 1.5 m apart from each other and 5–7 cm in diameter. Near the opening of each hole, broken shells and opercula of *P. canaliculata* were discarded on the ground, as well as those of other snail species.

Collection of Snails

Apparently newly discarded shells and opercula of apple snails and other snail species were removed from the ground near the rat holes on 10 March 1998. After that, the rat holes were observed twice per day, once in the morning (between 0620 and 0730) and once in the evening (between 1800 and 1900) for 10 days to examine the frequency of predation per rat hole. When newly discarded shells or opercula were found, they were brought to the laboratory for species, size, and sex determination.

On 21 March, after the collection of discarded shells near the rat holes, we collected living snails up- and downstream in the canal near the holes (15 m along the stream and 1.5 m across). First, we collected all the snails on the surfaces of the canal (both on the concrete walls and on the sediment) within this area. We then collected snails buried in the sediment by sieving this material through hand nets with 5 mm mesh.

Shell Measurements

Shell heights were measured for all the *Pomacea* shells collected, both near the rat holes and in the canal. The length and width of broken shell parts were also measured for the individuals collected near the rat holes. Length was measured as the longest curvilinear distance of the broken part of the shell along the whorl. Width was measured vertical to the direction of the length (hence parallel to the shell axis), and measured three times along the whorl (twice near both ends and once in the middle) for each shell and then averaged.

Sexual dimorphism occurs in this apple snail: mature females have similar opercula and shell shapes to those of juveniles, but the opercula of mature males have reflected edges, and their shells have extended outer edges (Cazzaniga, 1990; Estebenet, 1998). Thus, sexes can be identified on the morphology of the shell or operculum after snails reach sexual maturity. Amongst a subsample of snails collected in the canal, all males 20 mm or larger in shell height had reflected operculum edges and fully developed testes (12 individuals dissected), and most (89%; 16/18) of the females in this size had well-developed albumen glands (cf. Kaneshima et al., 1986). Hence, for the snails collected from the canal, those with shell heights of 20 mm or larger were sexed, based on the morphology of the shell and operculum.

Sexes of the attacked snails were identified using only their opercula, since the outer edges of their shells were lost in most cases. Shell height for these snails also had to be estimated from the size of the operculum. The regression of operculum length on shell height was highly significant among snails in the canal (shell height = 1.458 \times operculum longitudinal length, r^2 = 0.968, n = 88, P < 0.0001). Using this regression equation, an operculum length of 13.7 mm corresponded to a shell height of 20 mm. Sex was thus determined for snails with discarded opercula of this size or larger.

RESULTS

Characteristics of Attacked Snails

We collected 196 discarded shells of *P. canaliculata* near the four rat holes. Most of the discarded shells were damaged and empty, whereas 19 shells (10%) were intact. Damaged snails were significantly larger (mean \pm SD shell height = 21.5 \pm 5.4 mm, n = 177) than intact ones



Figure 1

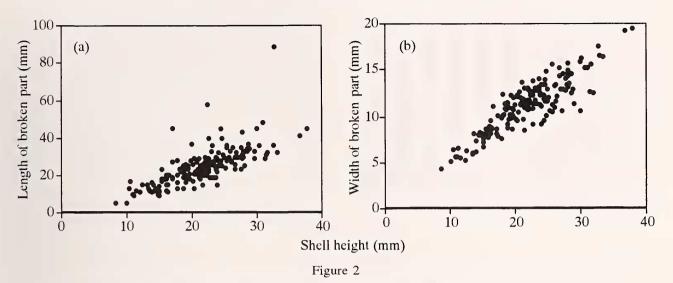
Shell of *Pomacea canaliculata* broken by the Norway rat, *Rattus norvegicus*. Shell height is 29 mm.

 $(11.9 \pm 5.6 \text{ mm}; t = 7.35, P < 0.0001)$. Most of these latter snails were still alive when collected.

The rats damaged the shells of apple snails in a characteristic way (Figure 1). All the damaged shells were broken from the outer edge along the whorl, and usually far less than one whorl was broken. The shapes of the broken parts were similar, irrespective of the shell height. Thus, there were significant correlations between shell height and the curvilinear length of the broken part along the whorl (n = 175: two cases were excluded in which the shell was broken so heavily that measurements were impossible, r = 0.726, P < 0.0001; Figure 2a), and between shell height and the width of the broken part (r = 0.877, P < 0.0001; Figure 2b). The flesh of the snails was completely eaten in most cases, except for the albumen gland of the female, which was discarded near the rat holes along with the broken shells.

Differences between Attacked Snails and Snails in the Canal

Shells of three species of freshwater snails were found near the rat holes (Table 1). The proportion of P. canaliculata was highest (88.7%), followed by the pleurocerid Semisulcospira libertina (Gould) (10.9%). Only one specimen of the vivipariid Cipangopaludina chinensis laeta (Martens) was found near the rat holes (0.5%). On the other hand, among snails living in the canal, the proportions of P. canaliculata (54.4%) and of S. libertina (45.5%) were similar. The proportion of these two major species varied significantly between the two sites (χ^2 =



Relationships of shell height to the length (a) and width (b) of the broken parts of shells of Pomacea canaliculata.

91.86, P < 0.0001) including all the snails collected. Although only snails that seemed newly discarded were collected at the start of the observations, some of these snails might have been there for a long time. If so, this difference between sites might have been due to changes in species composition over time rather than preference of rats. This possibility, however, could be refuted because the proportion of species varied significantly between snails in the canal and those near rat holes collected over the 10-day observation period ($\chi^2 = 18.89$, P < 0.0001).

The discarded *Pomacea* snails (mean \pm SD shell height = 20.5 \pm 6.1 mm, n = 196) were much larger than living conspecifics in the canal (10.6 \pm 5.1 mm, n = 612; t = 20.23 after log-transformation, P < 0.0001; Figure 3). Among the snails living in the canal, those on the surfaces (concrete walls and sediment) were larger (12.4 \pm 5.8 mm, n = 56) than those buried in the sediment (10.4 \pm 5.0 mm, n = 556; t = 2.85 after log-transformation, P < 0.01). The shells discarded near the rat holes were still much larger than the snails on the canal's surfaces (t = 10.03 after log-transformation, P < 0.0001). This last dif-

Table 1

Numbers of snails attacked by the Norway rat and living in the nearby canal.

	Snail species		
Site	Pomacea canaliculata	*	Cipangopaludina chinensis
Rat holes (total) Rat holes (collected	196 d	24	1
over 10 days) Canal	54 612	12 511	0 1

ference between sites was still significant even if snails collected at the start were excluded from the analysis (t = 5.49 after log-transformation, P < 0.0001).

The number of opercula found near the rat holes (n = 175) was similar to that of the empty shells without opercula (n = 184). The sex ratio estimated from the opercula should thus reflect the sex ratio of the attacked snails. The numbers of male and female opercula near the rat holes were 71 and 63, respectively, where operculum length was 13.7 mm or longer (corresponding to a shell

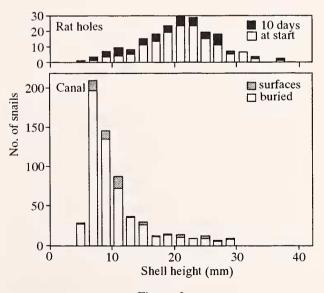


Figure 3

Size distributions of *Pomacea canaliculata* discarded near rat holes (upper) and those living in the canal (lower). Note that scales on the ordinate axis are different in the two graphs.

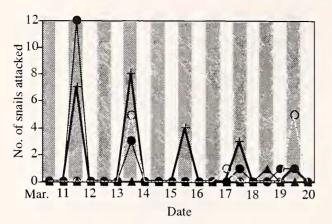


Figure 4

Numbers of *Pomacea canaliculata* attacked by rats, recorded at 12-hour intervals. Different symbols indicate different rat holes. Dark areas indicate night-time.

height of 20 mm or higher, including two intact males). The sex ratio for the discarded snails was not significantly different from the sex ratio of the snails collected in the canal (28:21, $\chi^2 = 0.25$, P = 0.62). This difference was also nonsignificant when the opercula collected at the start were excluded from the analysis ($\chi^2 = 0.32$, P = 0.57).

Frequency of Predation

The number of newly discarded shells recorded at 12-hour intervals varied between rat holes, sampling times, and days, from 0 (in most cases) to 12 (Figure 4). The average number of discarded shells per day per hole was 1.4. Attacks were much more frequent at night (n = 52) than in the day (n = 2; P < 0.0001, binomial test).

DISCUSSION

Most of the attacked shells of *P. canaliculata* were broken from the outer edge, and the size of the broken part was proportional to shell height, usually far less than one whorl. This pattern of damage suggests that the rats peeled off the shells with their teeth, until they reached the attachment site of the columellar muscle. A laboratory observation on the behavior of the rat confirmed this point. In addition, the rat avoided the albumen gland of the female snail. This was probably due to its bitter taste (based on the authors' personal tasting). In Colombia, the snail kite, *Rostrhamus sociabilis sociabilis*, is also known to discard the albumen gland of *Pomacea chemnitzi* when feeding (Snyder & Kale, 1983).

The rats attacked proportionally more *P. canaliculata* than *S. libertina* in the canal. The rats also preferred larger *P. canaliculata* to smaller ones. Feeding costs versus benefits may be relevant to these preferences. *P. canaliculata* is generally larger in size and has a thinner shell

than S. libertina. Rats would therefore gain more energy with far less effort by preying upon P. canaliculata. The broken area of the Pomacea shell is also a square function of shell height (since both length and width of the destroyed part are correlated with shell height), whereas body weight increases as a cubic function of length (at least in Pomacea dolioides: Bourne & Berlin, 1982). Thus, larger snails are likely to provide more benefit per effort for a rat. There was relatively little difference in size between male and female P. canaliculata in this study, and the rats showed no preference.

Many wild animals have been reported as predators of P. canaliculata, including leeches, aquatic insects, crabs, fishes, birds and mammals (Hamada & Matsumoto, 1985; Kondo & Tanaka, 1989; Ozawa et al., 1989; Halwart, 1994a, b; Chanyapate, 1997; Suzuki et al., 1999). In most cases, however, the impact of their predation is unknown, and few predators are known to feed on adult snails (with the exception of leeches; Ozawa et al., 1989). This study has shown that Norway rats prefer large P. canaliculata, and has suggested that at least on some occasions, predation rate may be quite high (e.g., 12 shells found at one rat hole in one night). In addition, laboratory observations showed that individual Norway rats can consume 68–72 adult snails (shell height = 20-30 mm) per day (n = 3; Yusa, personal observation). Considering its potentially high predation rate, preference for large snails, and wide distribution, the Norway rat seems likely to be one of the most important predators of the apple snail in the field. In fact, predation by rats (species not identified) has been noted as the main cause of the mortality of the apple snails in paddy fields at the International Rice Research Institute, the Philippines (Almazan et al., unpublished data). However, strong recommendation of this rat as a biological control agent is very unlikely, given that the rats themselves are serious pests of rice, and they can also be hosts of various bacteria or invertebrates parasitic to humans, including the rat lung worm, Angiostrongylus cantonensis, which uses P. canaliculata as an intermediate host and causes eosinophilic meningoencephalitis (Nishimura & Sato, 1986).

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